Journal of Forestry Research (2013) 24(2): 247–254
DOI 10.1007/s11676-013-0348-7

ORIGINAL PAPER

Comparing growth and fine root distribution in monocultures and mixed plantations of hybrid poplar and spruce

Lahcen Benomar • Annie DesRochers • Guy R. Larocque

Received: 2012-08-03; Accepted: 2012-10-15

Abstract: Disease prevention, biodiversity, productivity improvement and ecological considerations are all factors that contribute to increasing interest in mixed plantations. The objective of this study was to evaluate early growth and productivity of two hybrid poplar clones, *P. balsamifera* x *trichocarpa* (PBT) and *P. maximowiczii* x *balsamifera* (PMB), one improved family of Norway spruce (*Picea glauca* (PA)) and one improved family of white spruce (*Picea abies* (PG)) growing under different spacings in monocultures and mixed plots. The plantations were established in 2003 in Abitibi-Témiscamingue, Quebec, Canada, in a split plot design with spacing as the whole plot factor (1 × 1 m, 3 × 3 m and 5 × 5 m) and mixture treatments as subplot factor (pure: PBT, PMB, PA and PG, and 1:1 mixture PBT:PA, PBT:PG, PMB:PA and PMB:PG). Results showed a beneficial effect of the hybrid poplar-spruce mixture on diameter growth for hybrid poplar clones, but not for the 5 × 5 m spacing because of the relatively young age of the plantations. Diameter growth of the spruces decreased in mixed plantings in the 1 × 1 m, while their height growth increased, resulting in similar aboveground biomass per tree across treatments. Because of the large size differences between spruces and poplars, aboveground biomass in the mixed plantings was generally less than that in pure poplar plots. Leaf nitrogen concentration for the two spruce families and hybrid poplar clone PMB was greater in mixed plots than in monocultures, while leaf nitrogen concentration of clone PBT was similar among mixture treatments. Because of its faster growth rate and greater soil resources demands, clone PMB was the only one showing an increase in leaf N with increased spacing between trees. Fine roots density was greater for both hybrid poplars than spruces. The vertical distribution of fine roots was insensitive to mixture treatment.

Key words: *Picea glauca; Populus balsamifera* × *trichocarpa*; *P. maximowiczii* × *balsamifera*; mixed-species; monoculture; spacing; fine root

Fund project: This research was funded by Canada Economic Development, Quebec's Ministry of Natural Resources and Fauna (MRNF), the Natural Sciences and Engineering Research Council of Canada through a Collaborative and Research Development grant to AD, and the Program on Energy Research and Development of Natural Resources Canada.

The online version is available at http://www.springerlink.com

Lahcen Benomar (✉) • Annie DesRochers
Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable. Université du Québec en Abitibi-Témiscamingue, 341, rue Principale Nord, Amos, Qc, J9T 2L8, Canada. Email : Lahcen.benomar@uqat.ca; Tel: 1 819 762-0971; Fax: 1 819 797-4727

Guy R. Larocque
Natural Resources Canada, Laurentian Forestry Centre, 1055 rue du P.E.P.S., P.O. Box 10380, Stn. Sainte-Foy, Québec, Qc, G1V 4C7, Canada.

Corresponding editor: Hu Yanbo

Introduction

For the last two decades, short rotation forestry using fast-growing species has gained interest in response to worldwide increase in wood demand (FAO 2001). As a result, vast monoclonal plantations have been established in Europe and North America. Although monoculture plantations are easier to establish, tend and harvest, they are also associated with greater risks for diseases, such as those caused by fungal pathogens, e.g. *Melampsora sp.* (McCracken and Dawson 1997; Burdon 2001). In addition, environmental concerns of the public promote an unfavorable perception of monoclonal plantations, i.e. "social acceptability" (Hartley 2002; Howe et al. 2005). Scientists may also support the idea that monocultures have negative impacts on ecosystem functioning (Hooper et al. 2005; Kelty 2006; Knoke et al. 2008). Currently, polyclonal or mixed-species plantations are the most commonly proposed solutions to reduce risks associated with diseases (Roberds and Bishir 1997). Mixed plantations are attractive for several reasons, such as a potential increase in productivity (Kelty 2006; Nichols et al. 2006), diversification of final products (Nichols et al. 2006), habitat improvement for biodiversity (Felton et al. 2010), increase in recreational values, ecological sustainability and ecosystem resilience (Hartley 2002; Knoke et al. 2008). However, forest managers are hesitant to establish mixed plantations, because of a lack of data on productivity of mixed-species plantations and conservative attitudes regarding management and harvesting of this type of plantation (Nichols et al. 2006).

Theoretically, there are three types of interactions between species in mixed stands that can increase productivity: facilitation, complementarity and sampling effect (Aarssen 1983;

Loreau et al. 2001). Facilitation occurs when one species benefits from the presence of another species. The most common and well-studied example supporting this ecological principle in forest plantations is the mixture of *Eucalyptus sp* with the nitrogen-fixing species of Acacia, where the mixture provided a high level of productivity comparatively to mono-specific plantations of *Eucalyptus sp* (Bauhus et al. 2000; Binkley et al. 2003). Facilitation can also take place when litter decomposition of one species is accelerated by the presence of the other species' litter (Gartner and Cardon 2004; Forrester et al. 2006). This is mainly due to the fact that mixing leaves from different species affects the biological, chemical and physical aspect of the litter (Gartner and Cardon 2004). The complementarity hypothesis, also called competitive reduction, refers to conditions of interspecific competition that are more favourable than intraspecific competition through niche separation and more efficient use of site resources in mixtures than in mono-specific cultures. This occurs when combinations of species in mixtures differ in shade tolerance, phenology, duration of photosynthetic activity and height growth rates, which may lead to canopy stratification contributing to an increase in light capture efficiency at the canopy level. Niche differentiation may also occur when species differ in their rooting depth leading to a more efficient use of soil resources which may improve the nutritional status of trees. Several results in forest plantations have shown a positive effect of canopy stratification (Menalled et al. 1998; Kelty 2006) and differential distribution of roots (Jose et al. 2006; Ewel and Mazzarino 2008) on productivity. Lastly, the sampling effect theory suggests that species mixtures may have a chance of containing one or more over-yielding species which in turn would be largely responsible for an overall productivity increase of the mixture (Loreau et al. 2001; Hooper et al. 2005).

The main goal of this study was to compare the productivity of monoculture and mixed plantations of hybrid poplar and white and Norway spruce (mixture spruce-hybrid poplar: 1:1). We hypothesized an increase in productivity in mixed plantations compared to monocultures of the poplars/spruces through spatial niche differentiation. Our hypothesis was based on two assumptions: The first assumption was that slow growth and shade tolerance of spruce and fast growth and shade intolerance of hybrid poplar would lead to the formation of two layers in the canopy, reducing competition for light within the canopy. The second assumption was that there would be a vertical differentiation (spatial compartmentalization) of fine roots between spruce and hybrid poplar in mixed plantations, allowing species to use soil resources differentially and more efficiently which may improve the nutritional status of trees.

Materials and Methods

Study area

The study area was located in the boreal region of Abitibi-Témiscamingue, Quebec, Canada. Three sites were randomly selected for this study: Amos (48°36'N, 78°04'W), Rivière Héva (48°11'N, 78°16'W), and Nédelec (47°45'N, 79°22'W). The Amos site was an abandoned farmland with heavy clay soils dominated by grasses and a few patches of alder (*Alnus incana* ssp. rugosa), willow (Salix spp.) and trembling aspen (*Populus tremuloides* Michx.). Rivière Héva was also an abandoned farmland with heavy clay soils, dominated by shrubs and a few patches of alder, willow and trembling aspen. Nédelec was previously dominated by a trembling aspen forest that had been commercially harvested in 2000. The main species that were present included, in addition to trembling aspen, white birch (*Betula papyrifera* Marsh.) and pin cherry (*Prunus pensylvanica* L.) growing on a sandy-loam textured soil.

The plantations were established in 2003. Two hybrid poplar clones (*P. balsamifera* x *trichocarpa* (PBT) and *P. maximowiczii* x *balsamifera* (PMB)), one improved white spruce family (*Picea glauca* (PG)) and one improved Norway spruce family (*Picea abies* (PA)) were used. Each hybrid poplar clone and spruce family was planted in both monoculture and mixed plantations under 3 spacings: 1 × 1 m, 3 × 3 m and 5 × 5 m. The experiment was designed as a split-plot layout with spacing as the whole plot factor and each site as a replicate. Each spacing was sub-divided into eight mixture treatments (sub-plots): monoculture of PBT, PMB, PA and PG, and mixed (ratio 1:1) PBT:PA, PBT:PG, PMB:PA, and PMB:PG (Fig. 1). Size of the experimental units (plots) was related to spacing (25 m^2, 225 m^2 and 625 m^2), and contained 36 trees (6×6 rows of trees). Plots were distanced a minimum of 3 m to allow machinery travel between plots. Additional information can be found in Benomar et al. (2011).

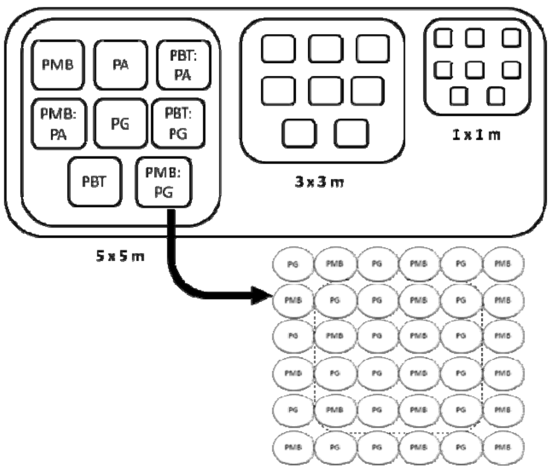

Fig. 1 Schematic representation of the experimental design with spacing as whole plot and mixture treatment as subplot units and the trees arrangement within mixed plots. Only the inner 16 trees were used for measurements (dotted line).

Growth

Total height, stem basal diameter (D: 10 cm above soil), diameter at breast height (DBH) and survival were measured at the end of the sixth growing season (mid-October 2008). Trees that died in 2003 and 2004 were replaced in 2005 to maintain competition levels representative of the spacing. However, the replacement

trees were not included in the analyses. Cumulative biomass production after six growing seasons was estimated using biomass equations from Benomar et al. (2012) for hybrid poplar clones and Ter-Mikaelian and Parker (2000) for the spruces. Above-ground biomass production at the plot level (Mg dry mass ha^{-1}) was estimated without consideration of mortality by multiplying tree mean above-ground biomass with tree density at planting. This is because competition- induced mortality did not yet occur in the plantations. Mean survival was similar across the different treatments and greater in the 1×1 m and 3×3 m spacings (90%) than in the 5×5 m spacing (67%). The higher mortality in the 5×5 m spacing was probably due to animal browsing (moose and voles), machinery damage or perhaps higher wind velocity.

Foliage nitrogen

During the first week of August 2008, two to three leaves per poplar tree and needles from two to three terminal shoots per spruce were sampled in the upper section of the crown of one representative tree within each treatment. After oven-drying (72 °C for 72 h), samples were ground using a Wiley mill (Model 3383-L10, Thomas Scientific, Swedesboro, NJ, USA), equipped with a 0.4-mm mesh sieve. Leaf nitrogen was determined by high-temperature combustion using a LECO elemental analyser (CNS2000, Leco Corp., St. Joseph, MI) at the Forest Resources and Soil Testing Laboratory, Lakehead University (Thunder Bay, ON, Canada).

Fine roots distribution

Root sampling was conducted on June 10, July 15, and September 15, 2008. These dates corresponded approximately to the beginning, middle and end of the growing season, respectively. One tree was randomly selected within each pure sub-plot and one tree from each species within each mixed sub-plot. For logistical reasons, roots were not sampled in the PA, PBT:PA and PMB:PA plots. For each selected tree, soil coring was performed in two directions. For each direction, a soil core was taken at three distances from the trunk of the tree for the 1×1 m spacing (10 cm, 30 cm and 50 cm) and at four distances from the trunk for the 3×3 m and 5×5 m spacings (10 cm, 30 cm, 50 cm and 150 cm). Depth at which the cores were taken was first fixed to 60 cm, but since very little roots were found below 40 cm, we limited the coring depth to 40 cm after the first sampling at Amos (June). A total of 920 soil cores were collected. Each soil core was divided into two depth classes: 0–20 cm and 20–40 cm. Samples were placed in plastic bags and stored at -4°C until analysis (maximum of 1 week): Fine roots (< 2 mm) were separated from soil by washing the cores delicately. Live roots were distinguished from dead roots by colour and flexibility, before oven-drying for three days for biomass determination. Spruce, poplar and grass roots were easily distinguished from each other by color and morphology.

Statistical analyses

Data were analyzed using the Statistical Analysis System (SAS Inc., 2000). Response variables such as diameter, height, cumulative aboveground biomass, and leaf nitrogen concentration were analyzed using the following general linear mixed effects model:

$$Y=\mu+\beta_s+\beta_m+\beta_{s*m}+E_{site}+E_{site*spacing}+E_{site*s*m}+\varepsilon \quad (1)$$

where Y is the response variable, μ the grand mean: β_s the fixed effect of spacing (1 × 1m, 3 × 3m and 5 × 5m), β_m the fixed effect of mixture treatment, β_{s*T} the fixed effect of the interaction between spacing and mixture, E_{site}, $E_{site*spacing}$ and $E_{site*s*m}$ are the random effects for site, whole plot and subplot respectively. E_R is the residual error. Data were log-transformed to achieve the assumptions of normality and homoscedacity of residuals. Fine root density was analyzed using the following general linear mixed effects model:

$$\begin{aligned}Y=&\mu+\beta_s+\beta_m+\beta_{s*m}+\beta_d+\beta_{s*d}+\beta_{m*d}+\beta_{s*m*d}+\beta_{time}+\\&\beta_{s*time}+\beta_{m*time}+\beta_{d*time}+\beta_{s*m*time}+\beta_{s*d*time}+\\&\beta_{m*d*time}+E_{site}+E_{site*s}+E_{site*s*m}+\varepsilon\end{aligned} \quad (2)$$

where Y is the fine root density, μ the grand mean, β_{time} the fixed effect of time of soil coring (June, July and September), β_d the fixed effect of soil depth (0-20cm and 20-40cm), β_{s*d} the fixed effect of interactions between spacing and depth, β_{m*d} the fixed effect of interactions between mixture and depth, β_{s*m*d} the fixed effect of interactions between spacing, mixture and depth, β_{s*time} the fixed effect of interactions between spacing and time, β_{m*time} the fixed effect of interactions between mixture and time, β_{d*time} the fixed effect of interactions between depth and time, $\beta_{s*m*time}$ the fixed effect of interactions between spacing, mixture and time, $\beta_{s*d*time}$ the fixed effect of interactions between spacing, depth and time, $\beta_{m*d*time}$ the fixed effect of interactions between mixture, depth and time and others symbols are as in Eq1. Root square transformation of the data was necessary to achieve model's assumptions. The proportion of area at each horizontal position was used as a weighting factor. The weighting factors for the 1×1 m spacing were 0.04, 0.32 and 0.64 for 10, 30 and 50 cm, respectively. The factors for the 3×3 m spacing were 0.0044, 0.04, 0.071 and 0.88 for 10, 30, 50 and 150 cm, respectively. For the 5 × 5 m spacing, the weighting factors were 0.0016, 0.0128, 0.0256 and 0.8 for 10, 30, 50 and 150 cm, respectively. Means were compared by Tukey's multiple range tests for all possible comparisons and differences were considered significant at $p\leq0.05$.

Results

Growth

Cumulative aboveground biomass estimated at stand level after six growing seasons (Mg dry mass ha^{-1}) was strongly affected by both spacing (p<0.001) and mixture treatment (p<0.001). The

increase of spacing between trees strongly decreased stand aboveground biomass in all plots (Table 1). Hybrid poplar-spruce mixtures generally produced less aboveground biomass per hectare than pure hybrid poplar plots, except the mixture of PMB:PG in the 1×1 m spacing. The two spruce species produced similar amounts of biomass which was very low compared to the hybrid poplar clones and contributed very little to the total plot biomass on a per hectare basis in mixtures with poplars.

Table 1. Above ground biomass production after six growing seasons of two hybrid poplar clones (PBT and PMB) and two spruce families (PA and PG) growing in monocultures and mixed plots at three spacings (1×1 m, 3 × 3 m and 5 × 5 m).

Spacings	mixtures	Aboveground biomass (Mg dry mass ha^{-1})				
		PBT	PMB	PA	PG	Total
1x1m	PBT	26.6(3.21)a	-	-	-	26.5(3.21)a
	PBT:PA	12.6(2.62)b	-	1.50(0.12)b	-	14.1(1.04)b
	PBT:PG	12.8(4.65)b	-	-	1.56(0.31)b	14.3(4.65)b
	PMB	-	29.8(4.87)a	-	-	29.8(4.87)a
	PMB:PA	-	17.7(2.71)b	1.46(0.12)b	-	19.1(2.51)b
	PMB:PG	-	25.9(5.13)ab	-	1.48(0.13)b	27.6(5.03)a
	PA	-	-	4.39(0.49)a	-	4.4(0.49)c
	PG	-	-	-	3.95(0.72)a	4.0(0.72)c
3x3m	PBT	3.10(0.30)a	-	-	-	3.1(0.30)c
	PBT:PA	1.49(0.41)b	-	0.44(0.02)b	-	1.9(0.47)d
	PBT:PG	1.62(0.45)b	-	-	0.27(0.07)b	1.9(0.25)d
	PMB	-	6.87(2.12)a	-	-	6.9(2.12)a
	PMB:PA	-	4.01(2.47)b	0.21(0.07)c		4.2(2.31)bc
	PMB:PG	-	4.85(3.12)b	-	0.29(0.03)b	5.1(3.05)ab
	PA	-	-	0.63(0.15)a	-	0.6(0.15)e
	PG	-	-	-	0.62(0.04)a	0.6(0.04)e
5x5m	PBT	1.21(0.33)a	-	-	-	1.2(0.33)c
	PBT:PA	0.76(0.36)a	-	0.09(0.01)b	-	0.9(0.01)c
	PBT:PG	0.35(0.12)b	-	-	0.14(0.04)b	0.5(0.11)d
	PMB	-	4.53(1.40)a	-	-	4.5(1.40)a
	PMB:PA	-	2.03(0.24)b	0.13(0.04)a	-	2.5(0.00)b
	PMB:PG	-	1.81(0.87)b	-	0.10(0.04)b	1.9(0.80)bc
	PA	-	-	0.17(0.01)a	-	0.2(0.01)d
	PG	-	-	-	0.21(0.07)a	0.2(0.07)d

Within spacing and column, means sharing the same letters are not significantly different at $p \leq 0.05$. Numbers in parentheses are standard errors of the mean. PBT: hybrid poplar clone PBT. PMB: hybrid poplar clone. PA: Norway spruce family. PG: white spruce family.

Spacing and mixture treatment did not affect biomass accumulation on a per tree basis for clone PBT, except in the PBT:PA mixture in the 5 × 5 m spacing where trees produced a little more biomass (Fig. 2a). On the other hand, mixture treatment greatly affected aboveground biomass per tree for clone PMB, where it was greater in the PMB:PG mixture in the 1×1 and 3×3 m spacings (Fig. 2b). Aboveground biomass accumulated in the two spruce species was very small after six years compared to the poplars, and was unaffected by changes in spacing and mixture (Figs. 2c, 4d).

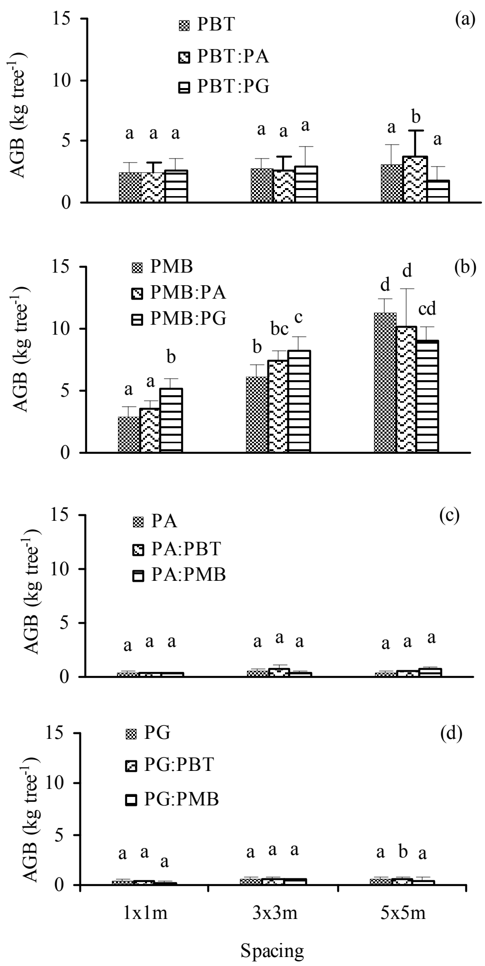

Fig. 2 Aboveground biomass (AGB) after six growing seasons of (a) hybrid poplar clone PBT, (b) hybrid poplar clone PMB, (c) Norway spruce family (PA) and (d) white spruce family (PG) growing in monocultures and mixed plots at three spacings. Means sharing the same letters are not significantly different at $p \leqslant 0.05$. Bars represent standard errors of the mean.

The two hybrid poplar clones responded similarly to spacing and mixture treatment in terms of basal diameter after six years; it increased significantly with the increase in spacing and was greater in mixtures compared to pure plot in the 1 × 1 m and 3 × 3 m spacings (Figs. 3a, b). Unlike diameter growth, the two clones responded differently to spacing and mixture in height growth: Trees of clone PBT were taller in the 1×1 m spacing compared to the 3×3 and 5×5 m spacings, with no significant effect of mixture treatment (Fig. 3e). In contrast, trees of clone PMB were generally taller in the two largest spacings compared to the 1×1 m spacing (Fig. 3f). For Norway spruce (PA), basal diameter was slightly reduced when mixed with hybrid poplar in the 1×1 m spacing, while basal diameter was similar among mixtures in the 3 × 3 m and 5 × 5 m spacings (Fig.3c). However, PA trees in mixed plantings were taller in the 1 × 1 m spacing (Fig. 3g). White spruce (PG) showed less variability than PA in basal diameter among spacings and mixtures (Fig. 3d), but also

had a greater height in mixed plots in the 1 × 1 m spacing compared to the rest of the treatments (Fig. 3h).

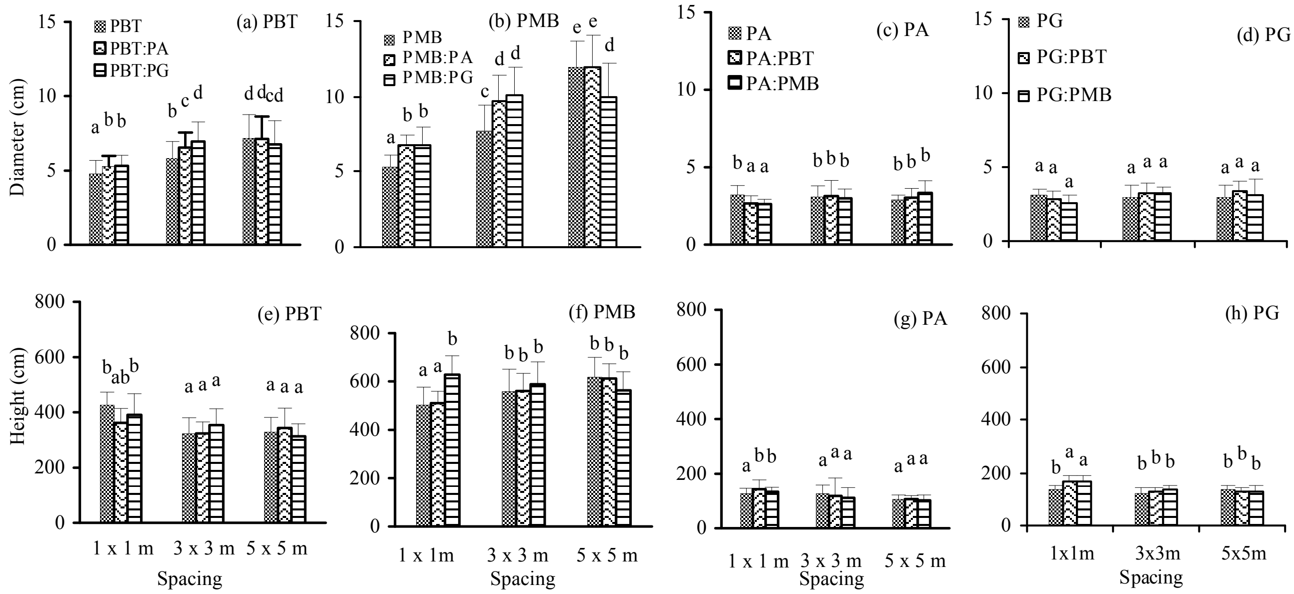

Fig. 3 Basal diameter and height after six growing seasons of hybrid poplar clones PBT and PMB and white and Norway spruce (PG and PA, respectively) families growing at three spacings in monocultures and mixed plots. Means sharing the same letters are not significantly different at $p \leqslant 0.05$. Bars represent standard errors of the mean.

Leaf nitrogen

The response to both spacing and mixture treatments in terms of leaf nitrogen concentration ($mg \cdot g^{-1}$) was different among spruce species and hybrid poplar clones. Clone PBT had similar leaf N across spacings and mixtures (Fig. 4a), while clone PMB had greater leaf N concentrations when planted in mixed compared to pure plot (Fig. 4b). Leaf N concentrations also increased significantly from the 1 × 1 m to 5 × 5 m spacing in pure plots and from the 1 × 1 m to 3 × 3 m spacing in mixed plots for this clone (Fig. 4b). Leaf N concentrations of clone PMB were similar whether the spruce was PG or PA in the 1 × 1 m and 3 × 3 m spacings, however in the larger spacing, leaf N of the PMB poplar was greater when mixed with PA than with PG. Leaf N concentrations were similar for PA and PG and across spacings and mixture treatments, except in pure plots at the 1 × 1 m spacing where leaf N concentrations were the lowest (Fig. 4c, d).

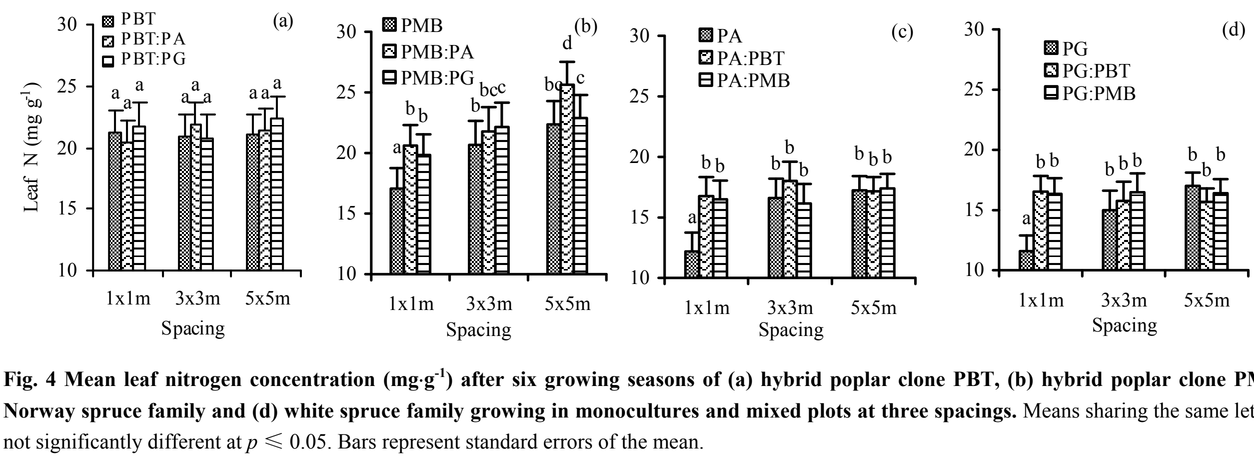

Fig. 4 Mean leaf nitrogen concentration ($mg \cdot g^{-1}$) after six growing seasons of (a) hybrid poplar clone PBT, (b) hybrid poplar clone PMB, (c) Norway spruce family and (d) white spruce family growing in monocultures and mixed plots at three spacings. Means sharing the same letters are not significantly different at $p \leqslant 0.05$. Bars represent standard errors of the mean.

Fine roots distribution

Fine root density was much greater in the 1 × 1 m spacing comparatively to the other larger spacings, while there was no difference in fine root density between the 3 × 3 m and 5 × 5 m spacings (Table 2). The time of sampling had no significant effect on fine root density (p>0.05). Mixture treatment had a significant effect on fine root density only in the 1 × 1 m spacing, where the

two hybrid poplar clones had greater fine root density in pure compared to mixed plots (Table 2). White spruce, in contrast, had similar fine root densities in mixed and pure plots across the spacings (Table 2). Fine root density was the greatest for PMB followed by PBT and PG. The vertical distribution of fine root density was similar across spacings and mixture treatments, and decreased from 0–20 cm to 20–40 cm depth by 42, 55 and 68% for PBT, PMB and PG respectively in the 1 × 1 m spacing and by 55%, 48% and 65% for PBT, PMB and PG respectively in the 3 × 3 m and 5 × 5 m spacings.

Table 2. Vertical distribution of fine root density (g·dm^{-3}) for hybrid poplar clones (PBT and PMB) and for white spruce (PG) growing at three spacings (1 × 1 m, 3 × 3 m and 5 × 5 m) in monocultures and mixed plantations after six growing seasons.

	1 × 1 m		3 × 3 m		5 × 5 m	
	mixed	monoculture	mixed	monoculture	mixed	monoculture
			0–20cm			
PBT	17.1b	23.2a	1.3c	1.5c	0.9d	1.3c
PMB	31.5b	39.8a	2.1c	2.4c	1.7c	1.9c
PG	10.3a	11.3a	0.9b	1.0b	0.8b	1.0b
			20–40cm			
PBT	9.6b	14.5a	0.6c	0.8c	0.4d	0.7c
PMB	13.1b	17.7a	1.1d	1.5c	0.9d	0.9d
PG	3.8a	3.7a	0.4b	0.4b	0.3b	0.4b

Means sharing the same letters are not significantly different at $p < 0.05$.

Discussion

Growth and stand productivity: mixtures *vs* monocultures

Diameter of the poplars were slightly greater when mixed with spruces compared to pure plantings, which resulted in a slight increase in aboveground biomass on a per tree basis for clone PMB. The increase in basal diameter of hybrid poplars in mixed plantings in the smaller spacings probably arises from a reduction in competition, especially for light, through canopy stratification with the spruces. Although it may seem that the competitive reduction hypothesis or "complementarity" (Aarssen 1983) applies at this stage of stand development, it most likely reflects only a decrease in intraspecific competition since there was only half the number of poplars in mixed plantings and also since the spruces were so small, exerting little interspecific competition. This could also be seen as an early example of the sampling effect (Loreau et al. 2001; Hooper et al. 2005), where one species, such as a hybid poplar, takes advantage of the mixture and is largely responsible for an increase in overall productivity of the plots. The productive advantage of mixed stands showing a stratification of the canopy in natural forest is still controversial. Mixtures of shade tolerant and shade intolerant species in boreal regions, for example, can have equivalent (Cavard et al. 2010; Chen and Klinka 2003), or greater (Chen et al. 2003; Légaré et al. 2004; Man and Lieffers 1999) productivity. This controversy is due to variations in site quality, stand density, stand developmental stage and proportion of each species within mixtures that affect the evolutionary interspecific interactions between species (Man and Lieffers 1999; Chen et al. 2003; Amoroso and Turnblom 2006). In our study, the mixtures of PBT:PG, PBT:PA and PMB:PA were less productive than pure plots of hybrid poplar clones across spacings, simply due to the relative much smaller size of the spruces compared to the poplars. The PMB:PG mixture had similar aboveground biomass than the pure PMB plots, due to a greater increase in aboveground biomass in a per tree basis for trees of clone PMB in this mixture, while clone PBT was inefficient in taking advantage of the greater canopy space available in the mixed plantings. Our data does not allow us to pose a plausible hypothesis on why PMB was more productive in the mixed plantings with PG but not with PA. Since the spruces find themselves quickly overtopped by poplars in mixed plantings, it was not surprising to find an effect of the mixture treatment on diameter and height growth. In the 1 × 1 m spacing where the canopy was closed, trees compensated by growing taller while their diameter growth slightly decreased, which translated into no significant difference in aboveground biomass per tree across mixture treatments for the spruces. However because the plantations are relatively young (i.e. canopies were not fully closed in the 3 × 3 m and 5 × 5 m spacings), competitive relationships will likely become more significant in the future. Nevertheless, one can observe early the benefits of mixed plantings on spruce wood quality in the 1 × 1 m spacing, due to their reduced taper, and later perhaps a reduced branching and ratio of juvenile to mature wood (Jozsa and Middleton 1997).

Height growth and canopy stratification

Shade intolerant species usually exhibit greater initial height growth comparatively to shade tolerant species. Shade tolerant species also usually have a good ability to survive under low light conditions (Kelty 2006). Differences in early height growth thus generally lead to canopy stratification in mixture of these two types of species under natural conditions (Kabzems et al. 2007). In this study, the hybrid poplar trees were very tall (3.5 to 7 m) compared to either spruce species (< 2 m) , which indeed lead to canopy stratification in the mixed plantings.

Height growth is not expected to change in mixed or pure plantings (Amoroso and Turnblom 2006) and is expected to remain insensitive to changes in spacing between trees, except perhaps at very narrow or wide spacings (Lanner 1985). The increase in height we observed in the closest spacing for the spruces in mixed plantings and for clone PBT is a result of greater allocation of carbon to height rather than diameter in response to an increase in competition for light (Grams and Andersen 2007). Conversely, more carbon is allocated to diameter than height at very wide spacings (Sumida et al. 1997). This was not observed for clone PMB, which could be explained by a greater importance of below-ground competition than aboveground competition for this clone (Grams and Andersen 2007).

Fine roots distribution

Stratification of fine roots in mixed stands is supposed to reduce interspecific competition for soil resources such as nitrogen and water and consequently increase overall stand productivity (Man and Lieffers 1999; Jose et al. 2006). This was found, for example, in Norway spruce and European beech (*Fagus sylvatica*) mixed stands (Schmid and Kazda 2002; Bolte and Villanueva 2006) and in larch-ash (*Larix gmelini-Fraxinus mandshurica*) mixtures (Cui 1997; Wang 2002). Results in this study showed a similar trend in fine root distribution in all treatments with a greater fine root density at the soil surface and less in deeper soil (20-40 cm). The slow growth of spruces and low fine root density implies they have much lower demands in soil resources compared to the poplars in mixed plantings, and consequently exert low interspecific competition for belowground resources. Hence, the fact that roots of the two species occupied the same soil strata at this age of the plantation may only be the result of an absence or low interspecific competition. Perhaps stratification of the root systems will occur as the plantations age and interspecific competition increases (Casper and Jackson 1997; Rothe and Binkley 2001). Root stratification in mixed stand of Norway spruce and European beech for example, was generally observed in mature stands (Schmid and Kazda 2002; Bolte and Villanueva 2006).

Leaf nitrogen

Because leaf N reflects soil N availability, leaf N can be an indirect measure of belowground competition (Ordoñez et al. 2009). We did not find a change in leaf N in response to both mixture and spacing treatments for clone PBT, suggesting an absence of intra- or interspecific competition for soil N. In contrast, leaf N of clone PMB was very sensitive to both spacing and mixture treatment. This clone grew faster than clone PBT and probably had greater demands for soil N and resulted in a greater sensitivity to changes in spacing and mixture. Leaf N of clone PMB was greater when mixed with spruces, which probably resulted from the lesser need for N of the spruces and more available soil N for uptake by poplars. Interestingly, in the 1×1 m spacing, the spruce species also had greater leaf N in mixed plantings compared to monocultures. It could be argued that the presence of poplars increased N mineralization at the soil surface with its more-easily decomposed litter compared to spruce only litter (Gartner and Cardon 2004). However, since the plantations were mechanically tended (herbicide use is prohibited in forestry in Quebec) which does not remove all weeds close to the trees, we attribute this increase in leaf N in mixed plantings to the absence of weedy vegetation in these plots which was repressed by the presence of a dense poplar canopy in the 1×1 m spacing.

Conclusion

After six growing seasons, the growth of spruces was not affected by mixture treatment or spacing, while poplars had slightly better growth in mixtures (especially for clone PMB), through reduced competition between poplars in the mixed plantings. Reduced spacing however affected the taper of spruces, which could be a desirable trait for the forest industry. The two poplar clones behaved somewhat differently, which suggests that there is a need to properly select genotypes. Clone PMB rapidly took advantage of the available space in the larger spacings or in the mixtures with the spruces, which could be a desirable trait (high productivity) for mixed plantings if the spruces can tolerate to be overtopped until the poplars are ready for harvest. If not, then perhaps a clone such as PBT would be a better choice because of its more modest response to decreased competition offered by the spruces. Fine roots stratification under mixed plots did not occur at this stage of plantation development, but inter- and intra-specific competition caused by mixture treatments and spacings was well reflected in leaf N, especially for clone PMB. The present study does not reflect an operational design but rather, a test of coexistence ability between spruce and hybrid poplar.

Acknowledgements
We thank Réseau Ligniculture Québec, Norbord Inc., Alberta-Pacific Forest Industries Inc., CRSNG-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Center for Forest Management (CEF) and Natural Resources Canada, Laurentian Forestry Centre, for their support.

References

Aarssen LW. 1983. Ecological combining ability and competitive combining ability in plants: Toward a general evolutionary theory of coexistence in systems of competition. *Am Nat*, **122**(6): 707–731.

Amoroso MM, Turnblom EC. 2006. Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. *Can J For Res*, **36**(6): 1484–1496.

Bauhus J, Khanna PK, Menden N. 2000. Aboveground and belowground interactions in mixed plantations of *Eucalyptus globulus* and *Acacia mearnsii*. *Can J For Res*, **30**(12): 1886–1894.

Benomar L, DesRochers A, Larocque GR. 2011. Changes in specific leaf area and photosynthetic nitrogen-use efficiency associated with physiological acclimation of two hybrid poplar clones to intraclonal competition. *Can J For Res*, **41**(7): 1465–1476.

Benomar L, DesRochers A, Larocque GR. 2012. The effects of spacing on growth, morphology and biomass production and allocation in two hybrid poplar clones growing in the boreal region of Canada. *Trees Struct Func*, **26**(3): 939–949.

Binkley D, Senock R, Bird S, Cole TG. 2003. Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and nitrogen-fixing *Facaltaria moluccana*. *For Ecol Manag*, **182** (1-3): 93–102.

Bolte A, Villanueva I. 2006. Interspecific competition impacts on the morphology and distribution of fine roots in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.). *Eur J Forest Res*, **125**(1): 15–26.

Burdon RD. 2001. Genetic diversity and disease resistance: Some considerations for research, breeding, and deployment. *Can J For Res*, **31**(4): 596–606.

Casper BB, Jackson RB. 1997. Plant competition underground. *Annu Rev Ecol Syst*, **28**(1): 545−570.

Cavard X, Bergeron Y, Chen HYH, Paré D. 2010. Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests. *Can J For Res*, **40**(1): 37−47.

Chen HYH, Klinka K. 2003. Aboveground productivity of western hemlock and western red cedar mixed-species stands in southern coastal British Columbia. *For Ecol Manag*, **184** (1-3): 55−64.

Chen HYH, Klinka K, Mathey AH, Wang X, Varga P, Chourmouzis C. 2003. Are mixed-species stands more productive than single-species stands: An empirical test of three forest types in British Columbia and Alberta. *Can J For Res*, **33**(7): 1227−1237.

Cui XY. 1997. Spacial patterns of fine root abundance in mixed larch-ash plantation. *J Forestry Res*, **8**(4): 206−210.

Ewel JJ, Mazzarino MJ. 2008. Competition from below for light and nutrients shifts productivity among tropical species. *Proc Natl Acad Sci*, **105**(48): 18836−18841.

FAO. 2001. Global Forest Resources Assessment 2000. Main Report. FAO Forestry Paper. No 140 Rome, Italy

Felton A, Lindbladh M, Brunet J, Fritz Ö. 2010. Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. *For Ecol Manag*, **260**(6): 939−947.

Forrester DI, Bauhus J, Cowie AL, Vanclay JK. 2006. Mixed-species plantations of *Eucalyptus* with nitrogen-fixing trees: A review. *For Ecol Manag*, **233**(2-3): 211−230.

Gartner TB, Cardon ZG. 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos*, **104**(2): 230−246.

Grams TEE, Andersen CP. 2007. Competition for resources in trees: physiological *versus* morphological plasticity. *Prog Bot*, **68**(4): 356−381.

Hartley MJ. 2002. Rationale and methods for conserving biodiversity in plantation forests. *For Ecol Manag*, **155**: 81−95.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr*, **75**: 3−35.

Howe GT, Shindler B, Cashore B, Hansen E, Lach D, Armstrong W. 2005. Public influences on plantation forestry. *J For*, **103**(2): 90−94.

Jose S, Williams R, Zamora D. 2006. Belowground ecological interactions in mixed-species forest plantations. *For Ecol Manag*, **233**(2-3): 231−239.

Jozsa LA, Middleton GR. 1997. Les caractéristiques déterminant la qualité du bois: nature et conséquences pratiques. Forintek Canada Corp. Québec, Canada. 42 p.

Kabzems R, Linnell NA, Farnden C. 2007. Growing trembling aspen and white spruce intimate mixtures: Early results (13–17 years) and future projection. *J Ecosyst Manag*, **8**(1): 1−14.

Kelty MJ. 2006. The role of species mixtures in plantation forestry. *For Ecol Manag*, **233**(2-3): 195−204.

Knoke T, Ammer C, Stimm B, Mosandl R. 2008. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. *Eur J For Res*, **127**(2): 89−101.

Lanner RM. 1985. On the insensitivity of height growth to spacing. *For Ecol Manag*, **13**(3-4): 143−148.

Légaré S, Paré D, Bergeron Y. 2004. The responses of black spruce growth to an increased proportion of aspen in mixed stands. *Can J For Res*, **34**(2): 405−416.

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime J.P, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle A. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**: 804–808.

Man R, Lieffers VJ. 1999. Are mixtures of aspen and white spruce more productive than single species stands? *For Chron*, **75**(3): 505–513.

McCracken AR, Dawson WM. 1997. Growing clonal mixtures of willow to reduce effect of *Melampsora epitea* var. epitea. *Eur J For Pathol*, **27**(5): 319–329.

Menalled FD, Kelty MJ, Ewel JJ. 1998. Canopy development in tropical tree plantations: A comparison of species mixtures and monocultures. *For Ecol Manag*, **104**(1-3): 249−263.

Nichols JD, Bristow M, Vanclay JK. 2006. Mixed-species plantations: Prospects and challenges. *For Ecol Manag*, **233**: 383–390.

Ordoñez JC, Van Bodegom PM, Witte J-PM, Wright IJ, Reich PB, Aerts R (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Glob Ecol Biogeogr*, **18**(2): 137−149.

Roberds JH, Bishir JW. 1997. Risk analyses in clonal forestry. *Can J For Res*, **27**(3): 425−432.

Rothe A, Binkley D. 2001. Nutritional interactions in mixed species forests: a synthesis. *Can J For Res*, **31**: 1855−1870.

Schmid I, Kazda M. 2002. Root distribution of Norway spruce in monospecific and mixed stands on different soils. *For Ecol Manag*, **159**(1-2): 37−47.

Sumida A, Ito H, Isagi Y. 1997. Trade-off between height growth and stem diameter growth for an evergreen Oak, *Quercus glauca*, in a mixed hardwood forest. *Funct Ecol*, **11**(3): 300−309.

Ter-Mikaelian MT, Parker WC. 2000. Estimating biomass of white spruce seedlings with vertical photo imagery. *New For*, **20**(2): 145−162.

Wang QC. 2002. Spatial distribution of fine roots of larch and ash in the mixed plantation stand. *J Forestry Res,* **13**(4): 265−268.